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development to adults. When either hormone is low, the dauer state is promoted. Insulin/IGF and TGF- $\beta$  are expressed by sensory neurons in *C. elegans*, which couple transcription of both hormones to the environment. By contrast, downstream hormone receptors are broadly expressed, allowing for organism-wide developmental changes. Interestingly, the insulin pathway has also been linked to longevity, both in *C. elegans* and mammals, suggesting a link between stress-responses and aging, and that this 'lowly' worm can perhaps teach us something about human longevity as well.

**What remains to be explored?** We are only beginning to understand the molecular pathways that link development to environmental changes. While many of the molecular players may be organism-specific, some common themes may exist; for example, in metazoans, dedicated sensory cells may detect environmental stressors and alter systemic hormone pathways, as occurs in *C. elegans*. In addition, it remains unclear if these same developmental pathways are also linked to mechanisms controlling changes in animal behavior. It seems that in a worm eat worm world, coping with environmental stress by altering development can be the best way for some organisms to maximize genetic success.

#### Where can I find out more?

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### Reduced perceptual sensitivity for biological motion in paraplegia patients

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Many physiological and psychophysical studies suggest that the perception and execution of movement may be linked [1–4]. Here we ask whether severe impairment of locomotion could impact on the capacity to perceive human locomotion. We measured sensitivity for the perception of point-light walkers — animation sequences of human biological motion portrayed by only the joints — in patients with severe spinal injury. These patients showed a huge (nearly three-fold) reduction of sensitivity for detecting and for discriminating the direction of biological motion compared with healthy controls, and also a smaller (~40%) reduction in sensitivity to simple translational motion. However, they showed no statistically significant reduction in contrast sensitivity for discriminating the orientation of static gratings. The results point to a strong interaction between perceiving and producing motion, implicating shared algorithms and neural mechanisms.

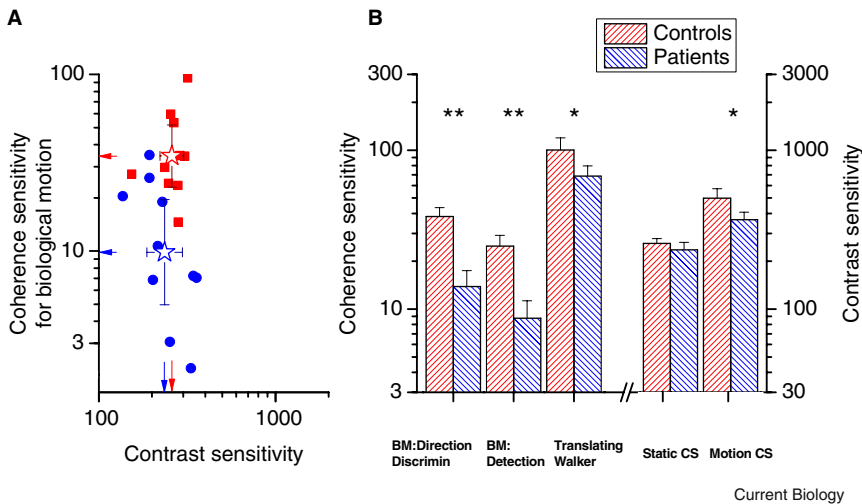
We measured sensitivity for discriminating the direction of ambulation of a 'point-light' walker (an animation sequence showing only the joints) in 16 patients with total lower-limb paralysis (with no concomitant head-injury) caused by adult spinal trauma at least nine months prior to testing, and also in 15 healthy controls. Random noise dots were added to the display, and sensitivity defined as the number of dots to yield 75% correct responses (see [5] and the Supplemental Movie). In ten patients, we also measured contrast sensitivity for discriminating the orientation or direction of a sinusoidal grating.

Figure 1A shows sensitivity for biological motion against orientation contrast-sensitivity, separately for patients (blue symbols) and controls

(red). While contrast sensitivity was clearly similar for the two groups (showing that there are no generalized perceptual impairments), sensitivity to biological motion was much reduced, by a factor of nearly three. Figure 1B plots average sensitivities for these and three other tasks: coherence sensitivity for detection of the point-light walker (choosing between a walker and an adjacent scrambled walker); coherence sensitivity for discriminating the direction of translation of a single frame of walker; and contrast sensitivity for discriminating the direction of motion of a 0.5 cycle/deg grating drifting at 8 Hz (16 deg/sec).

In both biological motion tasks (detection and direction-discrimination), average sensitivity for the patient group was greatly reduced compared with healthy controls, both by a factor of 2.8, which is highly statistically significant (one-tailed unpaired t-tests: detection  $t(29) = 3.63$ ,  $p = 0.0005$ ; direction discrimination  $t(29) = 3.79$ ,  $p = 0.0003$ ). Coherence sensitivity for translation of silhouette and the dynamic contrast sensitivity were also lower in patient than in controls, by about 40%, again statistically significant (coherence:  $t(29) = 1.80$ ,  $p = 0.04$ ; dynamic contrast sensitivity:  $t = 1.90$ ,  $p = 0.04$ ). This suggests that sensitivity to motion in general may be reduced in these patients, but less so than for biological motion. Static contrast sensitivity, on the other hand, showed no statistically significant impairment ( $t(18) = 0.81$ ,  $p = 0.21$ ), confirming that the reduced sensitivity for motion did not result from a generalised perceptual or cognitive deficit, or from reduced capacity to perform psychophysical tasks.

We also analysed the data by bootstrap sign-test, an assumption-free technique that takes into account the intra-subject variance (see Supplemental Information). For the two biological motion tasks, the significance level was  $p < 10^{-4}$ , meaning that on 10,000 independent samplings of the data, not one yielded higher average sensitivity for the patient group than the control. The difference in sensitivity of the translating walker was also significant ( $p = 0.009$ ), as was dynamic contrast sensitivity ( $p = 0.014$ ). Static contrast sensitivity, however,



**Figure 1.** Sensitivity of patients with paraplegia and healthy controls to motion stimuli. (A) Coherence sensitivity for perceiving the direction of ambulation of a point-light walker in noise, plotted against contrast sensitivity for detecting the orientation ( $\pm 45^\circ$ ) of 3 cycle/deg gratings. Blue and red points show data for individual patients and controls, respectively, and the stars the geometric means (error bars show 95% confidence limits). (B) Average sensitivity (geometric means) for five different psychophysical tasks. From left to right: coherence sensitivity for discriminating the direction of ambulation of a treadmill point-light walker; coherence sensitivity for discriminating scrambled from unscrambled point-light walkers; coherence sensitivity for discriminating the direction of translation of a single frame of walker; contrast sensitivity for detecting the orientation ( $\pm 45^\circ$ ) of a 2 cycle/deg sinusoidal grating; contrast sensitivity for detecting the direction of motion of a 0.5 cycle/deg grating drifting at 8 Hz (16 deg/sec). Two stars indicate that the sensitivity of patients was highly significantly less than controls (one-tailed t-test,  $p < 0.01$ ), one star significant ( $p < 0.05$ ).

remained clearly non-significant with the bootstrap test ( $p = 0.25$ ).

To test whether the impairment in biological motion was significantly more than that for simple translation, we divided the two sensitivity measures for biological motion by that for translational motion for all subjects, and repeated the bootstrap. In both cases, the normalized sensitivities for biological motion were significantly lower for the patient group (direction:  $p = 0.016$ ; detection:  $p < 10^{-4}$ ). We also performed various regression analyses between biological motion sensitivity and level of spinal injury, degree of motor impairment and time after injury (0.75–15 years), but none of these correlations was strong or significant.

Many researchers have suggested that vision is tightly linked to action, with ample evidence for a specialized ‘vision-for-action’ system [1]. A growing literature reports interactions between perceiving and executing movements. For example, performance in executing a particular sequence of arm movements improves as much with observation of the action as it does with physical practice [2]. Casile and Giese [3] showed the complementary effect:

production of a difficult and unfamiliar motor action (without visual feedback) improved subsequent perception of that action, demonstrating the influence of motor programs on perception of visual action. Perhaps the most dramatic evidence for the interconnection between perception and movement is the ‘mirror neurons’ of premotor and parietal cortices of human and non-human primates, which respond both when the monkey or person performs an action and when it observes the action of another [4].

Point-light biological motion sequences activate several specific visual regions, particularly the superior temporal sulcus (STS), a region of confluence of ventral and dorsal visual streams [6], but also active premotor areas in frontal cortex [7], areas very close to those described for the human ‘mirror system’ for action [8]. Although due caution is required in inferring causation from correlation, if premotor cortical function becomes reduced in long-term paraplegia (from functional disuse and neural atrophy and colonization [9]) it could explain why the patients show reduced sensitivity to biological motion, which

we intend to explore further with imaging studies. It is not clear why this should also impact on sensitivity for translational motion, but perhaps common circuits linked to motor control are involved in all types of motion perception. In any event, the results of this study provide clear evidence for important interactions between production and perception of motion, processes which are clearly less modular than often assumed [10].

#### Supplemental Information

Supplemental Information contains one Figure, one Movie and Supplemental Experimental Procedures and can be found with this article online at doi: 10.1016/j.cub.2011.09.048.

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